

Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon¹

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This paper describes differences in canopy arthropod community structure and herbivory between old-growth and regenerating coniferous forests at the H. J. Andrews Experimental Forest in western Oregon. Species diversity and functional diversity were much higher in canopies of old-growth trees compared with those of young trees. Aphid biomass in young stands was elevated an order of magnitude over biomass in old-growth stands. This study indicated a shift in the defoliator/sap-sucker ratio resulting from forest conversion, as have earlier studies at Coweeta Hydrologic Laboratory, North Carolina. These data indicated that the taxonomically distinct western coniferous and eastern deciduous forests show similar trends in functional organization of their canopy arthropod communities.

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Cet article expose les différences observées dans la structure communautaire des arthropodes du couvert foliacé et des herbivores entre des forêts de conifères de première venue et en régénération à la Forêt expérimentale H. J. Andrews dans l'ouest de l'Orégon. La diversité des espèces ainsi que la diversité fonctionnelle étaient beaucoup plus grandes dans les couverts foliacés des vieux arbres que dans ceux des jeunes arbres. La biomasse des aphides dans les jeunes peuplements dépassait d'un ordre de grandeur celle des vieux peuplements. Cette étude a montré l'existence d'un changement dans le rapport des insectes défoliateurs aux insectes piqueurs par suite de la succession forestière, tel que l'ont indiqué des travaux précédents effectués au Laboratoire d'hydrologie de Coweeta, en Caroline du Nord. Ces données montrent que les forêts conifériennes occidentales, taxonomiquement distinctes de celles de l'est, présentent des tendances similaires quant à l'organisation fonctionnelle de leurs communautés d'arthropodes vivant dans les couverts foliacés.

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Introduction

Responses of forest arthropods, especially pests and biological control agents, to forest management practices are not well-known. Previous studies have focused on responses of individual species of particular interest (Dyer 1986; Schowalter et al. 1986; Witcosky et al. 1986). Such studies have indicated that individual species respond in various ways to a given management practice, but have revealed little about the response of forest communities, which comprises distinct ecological strategies. Consequently, forest management practices designed to reduce populations of certain pests may inadvertently create new pest problems (Schowalter 1986).

Experimental study of arthropod responses to forest management is difficult for several reasons. The need for experimental manipulation in replicated plots often interferes with operational forest management. In addition, taxonomic complexity and difficulty of access, especially to forest canopies, hinder such study. Schowalter and Crossley (1987) compiled quantitative data from 8 watershed-years of study in eastern deciduous forests at Coweeta Hydrologic Laboratory in North Carolina. They noted that mature forest canopies tended to be dominated by defoliating arthropod species, while young forest canopies were dominated by sap-sucking species. Comparable data are not available for other forests.

Information on arthropod responses to natural forest succession and forest management is needed, especially in the Pacific Northwest, where vast tracts of undisturbed old-

growth forest are being rapidly converted to young managed forest, with largely unknown consequences for pest activity. The purpose of this study was to compare arthropod communities in old-growth and regenerating forest canopies in western Oregon.

Materials and methods

Site description

This study was conducted during 1986 at the H. J. Andrews Experimental Forest Long-Term Ecological Research Site, a 6100-ha research facility in the central western Cascades in Oregon. The forest is jointly operated by the USDA Forest Service Willamette National Forest and Pacific Northwest Research Station and by Oregon State University. Elevations range from 400 to 1500 m. A maritime climate prevails, with wet, relatively mild winters and dry, warm summers. Precipitation is strongly seasonal, with 75% occurring from November through March. Average annual precipitation is 2300 mm.

Vegetation at the Andrews Forest is dominated by relatively undisturbed old-growth forest with dominant trees >400 years old. Natural stands of mature trees about 140 years old also occur. A variety of experimental successional communities up to 30 years old have been created through logging and replanting. Old-growth trees are massive, commonly exceeding 70 m in height and 125 cm dbh. Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and western red cedar (*Thuja plicata* Donn) are the most abundant trees, accounting for about 40, 30, and 10% total cover, respectively (Franklin and Dyrness 1973; Grier and Logan 1977). Western hemlock is virtually absent from young stands, but maples (*Acer* spp.) and snowbrush (*Ceanothus velutinus* Dougl. ex Hook) are often abundant.

Six old-growth stands and six 7- to 11-year-old stands were selected for study on the basis of their distribution across the

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Andrews Forest. At each of the old-growth sites, one Douglas-fir (range in height 56-76 m, range in dbh 91-165 cm) and one western hemlock (range in height 49-64 m, range in dbh 64-81 cm) were rigged with pulleys and ropes for canopy access. The difficulty and expense of sampling these trees limited the sample size and sampling period. These trees were chosen from trees within 1-ha experimental plots on the basis of canopy dominance and safety for climbing. The young planted stands ranged in size from 2 to 13 ha and were bounded on one or more sides by old-growth forest. The young Douglas-fir trees were accessible from the ground (2-3 m height) and were sampled on a random basis. Because Douglas-fir is intolerant of shading, young Douglas-fir were not available for comparison in the old-growth stands. Western hemlock was not available for sampling in the young stands.

Each stand was sampled in mid-June (at budbreak), mid-August, and early October (near the end of the growing season) to represent seasonal changes in canopy arthropod communities. Each old-growth tree was sampled at upper, middle, and lower crown levels to represent within-tree variation. In the young stands, three randomly selected trees were sampled to represent the canopy arthropod community at each sampling time.

Sampling consisted of quickly enclosing a foliage-bearing branch in a 60-L plastic bag, clipping the branch, and sealing the bag. Some nocturnal or highly mobile insects might be undersampled by this technique, but the resident fauna of conifers is largely sedentary, and other quantitative sampling techniques, such as canopy fogging, are similarly biased (Wolda 1979).

Samples were chilled at 5°C until they could be processed in the laboratory, usually within a week. Individual branchlets were removed sequentially and examined for invertebrates. The bag was resealed between branchlet subsamples. Each branchlet was quickly examined for mobile arthropods, and then examined microscopically for smaller or less mobile arthropods. Finally, the bag was examined for remaining arthropods. Representative immatures were reared for adult identification. This method allowed organisms to be maintained live but inactive in bags until processing, permitted observation of feeding activity in many cases, and reduced the likelihood that dead arthropods would be overlooked. Arthropods were tabulated by taxon. Fresh weights of arthropods were recorded. Dry weights were estimated from dry weight to fresh weight ratios of subsamples to facilitate rearing and identification.

Foliage was examined for evidence of needle or bud consumption or damage. Numbers of buds and of buds killed by invertebrates were recorded. Numbers of needles missing or damaged by feeding were also recorded. Sampled plant material was dried at 45°C to constant weight. Foliage averaged 65% of the total dry mass in samples.

Arthropod population intensities (number per kilogram of sampled plant material) were pooled by tree species and site. Each of the three tree species \times age-class treatments had a sample size of 18 (6 sites \times 3 dates). These data for each arthropod taxon were transformed to the square root of intensity + 0.5 and analyzed by two-way ANOVA techniques (SAS Institute Inc. 1982), using tree species or age and date as main effects. Linear regression and correlation techniques (SAS Institute, Inc. 1982) were used to evaluate relationships between taxa. Degrees of freedom were adjusted as necessary to account for autocorrelation arising from resampling of old-growth trees (Milliken and Johnson 1984).

Results

Average arthropod population intensities on young Douglas-fir and old-growth Douglas-fir and western hemlock are shown in Table 1. All species except migrant arthropods (dispersing individuals of species that do not feed in conifer canopies) and some parasitic Hymenoptera were represented by relatively immobile feeding stages which could not escape collection. Although the extent to which the old-growth data reflect nominal conditions is unknown,

the young stand data are comparable with 4 previous watershed-years of data (e.g., *Adelges* at an intensity of 17 000/kg on one watershed in 1982) for the Andrews Forest (Schowalter et al. 1988).

Strong ($P < 0.05$) patterns of association with tree age, species, or season were found for several arthropod groups. The most dramatic differences were found for the Cooley spruce gall adelgid (a woolly aphid, *Adelges cooleyi* (Gillette), reproducing parthenogenetically in the absence of spruce), and a giant conifer aphid (*Cinara pseudotaxifoliae* Palmer) between young and old-growth Douglas-fir. Although highly variable, the mean intensities of these insects were three orders of magnitude greater on the young trees than on the old-growth trees. The highest intensity in the old growth was 173/kg compared with a minimum of 1800/kg in young stands. The hemlock woolly adelgid, *Adelges tsugae* Annand, was abundant on western hemlock.

Several arthropod taxa were significantly ($P < 0.05$) more abundant in old-growth canopies. Scale insects occurred almost exclusively on old-growth foliage >2 years old: *Nuculaspis californica* (Coleman) and *Chionaspis pinifoliae* (Fitch) on Douglas-fir; *C. pinifoliae*, *Stramenaspis kelloggi* (Coleman), and *Puto cupressi* (Coleman) on western hemlock. Defoliators, flower and seed predators, Neuroptera, predaceous mites, several spider taxa, and detritivores were also found exclusively in old-growth canopies. The predaceous neuropteran coniopterygids are considered rare, but immature *Semidalis* were collected from five old-growth Douglas-fir and three old-growth hemlock (8 of 12 trees) in August.

Within the old growth, several arthropods showed significant preferences for the two tree species. A bud moth, *Zeiraphera hesperiana* Mutuura and Freeman, was found feeding on newly expanding buds of old-growth Douglas-fir in June. A seed bug, *Kleidocerys* sp., occurred primarily on western hemlock cones. A salticid spider, *Metaphidippus aeneolus* (Curtis), and an oribatid mite, *Camisia carrolli* Andre, also were most abundant on old-growth hemlock. The data for old-growth canopies support earlier nonquantitative data from old-growth Douglas-fir (Mispagel and Rose 1978; Voegtlin 1982), but indicate that these earlier studies included arthropods, e.g., *Kleidocerys*, dispersing from other plant species.

Few significant ($P < 0.05$) interactions between taxa were revealed by these data. Surprisingly, aphids and ants were not significantly associated, contrary to many previous reports (Dixon 1985; Schowalter et al. 1981), although ants were observed tending aphids in young stands. Predaceous syrphid larvae were significantly associated with woolly aphids and other aphids in the old-growth samples and were frequently observed feeding on individuals of these species. Other trophic interactions may not have been apparent because of low numbers and small sample size. For example, predaceous cecidomyiid larvae (*Lestodiplosis* sp.) twice were observed prying loose the shells of scale insects and consuming the insects. An unidentified tachinid larva and an unidentified ichneumonid wasp emerged from *Zeiraphera* larvae.

Comparison of arthropod communities among tree species and age-classes indicated similar species richness and diversity on old-growth Douglas-fir and western hemlock, in contrast with young Douglas-fir. Diversity, measured by the Shannon-Weaver diversity index (Price 1984), was 2.3 for 66 species on old-growth Douglas-fir, 2.2 for 53 species on

TABLE 1. Arthropod intensities (number per kilogram) on regenerating (10-year-old) and old-growth (>400-year-old) Douglas-fir and western hemlock at the H.J. Andrews Experimental Forest in western Oregon

Arthropod group	Young Douglas-fir	Old growth	
		Douglas-fir	Western hemlock
Folivores			
Woolly aphids, <i>Adelges</i> (2 spp.)	23 000 (26 000)	48 (57)	39 (40)
Aphids, <i>Cinara</i>	100 (300)	0.4 (1.6)	0
Scales (4 spp.)	2 (8)	51 (41)	110 (100)
Budmoth, <i>Zeiraphera</i>	0	2.8 (6.0)	0
Other defoliators (5 spp.)	0	0.9 (1.9)	0.9 (1.9)
Flower and seed predators			
Thrips (2 spp.)	0	3.0 (3.8)	0.7 (1.8)
Seed bugs, <i>Kleidocerys</i>	0	1.1 (2.3)	17 (27)
Other seed predators (4 spp.)	0	0.4 (1.6)	0.9 (1.5)
Predators			
Ants, <i>Camponotus</i> (2 spp.)	2 (8)	0.7 (1.8)	0.2 (0.8)
Aphid predators (3 spp.)	7 (14)	1.5 (3.8)	0.6 (1.3)
Parasitic flies	0	0.2 (0.8)	0
Parasitic wasps (>6 spp.)	6 (13)	1.5 (2.9)	1.7 (3.5)
Predaceous Hemiptera (3 spp.)	4 (11)	2.4 (4.7)	0.2 (0.8)
Neuroptera, <i>Semidalis</i>	0	1.3 (2.6)	0.7 (1.8)
Predaceous mites (>3 spp.)	0	3.9 (5.7)	6.5 (6.4)
Spiders			
<i>Metaphiddipus</i>	6 (17)	1.3 (2.0)	3.3 (2.6)
<i>Apollophanes</i>	0	1.7 (3.3)	2.8 (3.7)
<i>Philodromus</i> (3 spp.)	0	1.7 (2.6)	1.3 (1.7)
<i>Anyphaena</i>	0	3.1 (3.9)	2.4 (2.8)
Other species (15)	6 (13)	2.8 (4.0)	5.7 (4.5)
Detritivores			
Springtails (Collembola)	0	0.7 (1.8)	0.2 (0.8)
Bark lice (Psocoptera)	0	0.6 (1.3)	17 (22)
<i>Camisia carrolli</i>	0	12 (16)	33 (22)
Other mites (5 spp.)	0	7.8 (8.9)	19 (14)
Migrant arthropods (6 spp.)	4 (11)	0.6 (1.3)	0.7 (1.4)

NOTE: Values are expressed as means, with standard deviation in parentheses.

western hemlock, and 0.04 for 15 species on young Douglas-fir.

The defoliating/sap-sucking herbivore mass ratio is an index of community function (Schowalter and Crossley 1987). Defoliator mass intensity (freshweight/dryweight = 0.2) was about 13 mg/kg in old-growth Douglas-fir and 3.0 in western hemlock, an order of magnitude less than in eastern deciduous forests (Schowalter and Crossley 1987). Sucking herbivore mass intensities were 0.75 mg/kg in old-growth Douglas-fir, 1.0 mg/kg in western hemlock, and 170 mg/kg in young Douglas-fir, within the ranges for mature and young eastern deciduous forests at Coweeta (Schowalter and Crossley 1987). The defoliator/sap-sucker ratios were 17, 3.0, and 0 for old-growth Douglas-fir, western hemlock, and young Douglas-fir, respectively. Defoliating insects dominated communities on older trees, while sap-sucking insects dominated on young trees, as was found in eastern deciduous forests at Coweeta (Schowalter and Crossley 1987).

The predator/herbivore mass ratios of 0.78, 2.5, and 0.12 for old-growth Douglas-fir, western hemlock, and young Douglas-fir, respectively, were also similar to those reported for eastern deciduous forests at Coweeta (Schowalter and Crossley 1987). Predator species richness and evenness were

much greater in the old growth than in the young growth. The disparity in predator diversity between old-growth and young canopies might be greater than the data indicate, because predators are relatively mobile and probably were undersampled in old growth more than in young stands (because of differences in the degree of foliage disturbance during sampling). The absence of several taxa of spiders was offset by an increase in *Metaphiddipus* in the young stands. The nonspider predators in the young stands were largely specialists on aphids. However, the effect of these predators on aphid abundance in young stands may have been limited by the aphid-tending ant *Camponotus modoc* Wheeler.

The numbers of species and individuals of detritivores indicate the presence of a significant arboreal detrital food web in old-growth forests. Some of these arthropods, especially mites, were observed feeding on yeast growth in bark crevices.

Although the sampling method could have underestimated abundances of some insects, most herbivores in these forests are relatively immobile. Measurable herbivory in the old growth was attributable primarily to *Zeiraphera*. Overall foliage loss was <1%, but *Zeiraphera* larvae consumed 14% (range 3–47%) of the buds on Douglas-fir. To assess tree response to this intensity of pruning (Dyer 1986), the mean

TABLE 2. Canopy arthropod biomass in old-growth and regenerating coniferous forests at the H.J. Andrews Experimental Forest in western Oregon

Functional group	Biomass (g/ha)	
	Old-growth forest	Regenerating forest
Defoliating herbivores	180	0
Sucking herbivores	10	370
Predators	160	50
Others	30	0
Total	380	420

dry foliage mass per expanding shoot for each Douglas-fir was measured in August, after shoot elongation had ceased. Bud mortality did not significantly affect foliage production per surviving shoot within the range observed in this study. These data suggest that pruning neither stressed the tree nor induced compensatory growth by surviving shoots.

The effect of aphid feeding on young trees could not be measured directly. At the lowest *A. cooleyi* intensity (1800/kg), <1% of the needles were affected. At intensities >50 000/kg, virtually all needles showed conspicuous tissue necrosis around feeding sites. Such injury can lead to considerable foliage loss (Furniss and Carolin 1977).

Arthropod biomass (Table 2) was estimated by multiplying calculated mass intensities by foliage biomass for representative stands: 8500 kg Douglas-fir foliage/ha and 1300 kg western hemlock foliage/ha in old growth (Grier and Logan 1977); 1400 kg Douglas-fir foliage/ha in a young stand (M. Klopsch, unpublished data from the H. J. Andrews Experimental Forest Long-term Ecological Research Site). The biomass of sucking arthropods in young stands was an order of magnitude higher than in old-growth stands. Aphid biomasses are comparable with aphid biomasses at Coweeta, but defoliator biomasses are considerably lower (Schowalter and Crossley 1987).

Discussion

Comparison of the results of this study with those compiled by Schowalter and Crossley (1987) for eastern deciduous forests at Coweeta indicates functional similarity between taxonomically distinct forest types but functional dissimilarity between early and late successional forests. Whereas herbivore biomass in old-growth conifer canopies was small and had primarily a pruning effect on the host (with negligible loss of plant mass), sucking herbivore biomass in the young stands was much larger. Aphid biomass in the young stands was sufficient to cause substantial needle necrosis, and possibly foliage loss, in trees with small standing crops of foliage. Similarly, Schowalter et al. (1981) reported that mature eastern deciduous forests normally supported small herbivore biomass, causing <7% biomass and nutrient loss; young forests supported sucking herbivore biomass comparable with that reported in this study, which is capable of mobilizing 25% of foliage standing crop biomass and 30% of foliage standing crop potassium. Larsson and Tenow (1980), Nielson (1978), Ohmart et al. (1983), and Reichle et al. (1973) also reported canopy dominance by defoliators and herbivory of <10% of standing crops in mature forests.

The results of this study support other studies indicating relatively insignificant herbivory in mature, structurally complex ecosystems compared with natural or planted monocultures (defined here, from a pest perspective, as predominantly host species). These studies suggest that widespread forest simplification will have serious consequences for pest management.

A structurally and functionally diverse ecosystem, such as these old-growth forests, maintains predator diversity and impedes herbivore success in discovering suitable hosts and completing development (Courtney 1986; Hunter and Aarssen 1988; Kareiva 1983; Risch 1981; Schowalter 1986; Visser 1986). Conversely, host monocultures created in the interior region by selective logging and fire suppression have proven vulnerable to mountain pine beetle, western spruce budworm, and Douglas-fir tussock moth (Schowalter 1986). The changes in diversity and environmental conditions accompanying harvest and replanting of young Douglas-fir monocultures in western Oregon also appear to be favorable to pests such as aphids (this study) and root beetles (Witcosky et al. 1986).

The combination of an abundant and suitable resource and an impoverished predator fauna in young monocultures could largely explain the dramatic difference in aphid populations between the young and old-growth stands. Interestingly, the lowest *A. cooleyi* intensities (but also low predator abundances) in young stands occurred at the two sites where maples and snowbrush, characteristic of early natural succession in these forests, were abundant. These data suggest that plant diversity in young stands could mitigate pest activity, perhaps by interfering with host discovery by dispersing insects. The potential for pest problems arising from current harvest and replanting rates on a regional level is substantial, given the long-term nature of forest management (Schowalter 1986).

The successional trends in canopy-arthropod community structure found in this study are similar to those found in taxonomically dissimilar eastern deciduous forests. This similarity suggests that common functional interactions occur during forest development, and increases the value of these studies for assessing the effects of forest succession or forest conversion on forest canopy communities. This study supports others which suggest that young forests are naturally susceptible to elevated activity of sap-sucking insects, a situation perhaps exacerbated by planting even-aged monocultures over extensive areas.

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- COURTNEY, S.P. 1986. The ecology of pierid butterflies: dynamics and interactions. *Adv. Ecol. Res.* **15**: 51-131.
- DIXON, A.F.G. 1985. *Aphid ecology*. Blackie and Son Ltd., London.
- DYER, M.I. 1986. The role of herbivores in forest ecosystems: the case for biosphere reserves. *In* The temperate forest ecosystem. *Edited by* H. Yang, Z. Wang, J.N.R. Jeffers, and P.A. Ward. Institute of Terrestrial Ecology, Cumbria, England. pp. 97-102.
- FRANKLIN, J.F., and DYRNESS, C.T. 1973. Natural vegetation of Oregon and Washington. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, OR.
- FURNISS, R.L., and CAROLIN, V.M. 1977. Western forest insects. U.S. Dep. Agric. For. Serv. Misc. Publ. No. 1339.
- GRIER, C.C., and LOGAN, R.S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. *Ecol. Monogr.* **47**: 373-400.
- HUNTER, A.F., and AARSSSEN, L.W. 1988. Plants helping plants. *BioScience*, **38**: 34-40.
- KAREIVA, P. 1983. Influence of vegetation texture on herbivore populations: resource concentration and herbivore movement. *In* Variable plants and herbivores in natural and managed systems. *Edited by* R.F. Denno and M.S. McClure. Academic Press, New York. pp. 259-289.
- LARSSON, S., and TENOW, O. 1980. Needle-eating insects and grazing dynamics in a mature Scots pine forest in central Sweden. *In* Structure and function of northern coniferous forests: an ecosystem study. *Edited by* T. Persson. *Ecol. Bull. (Stockholm)*, **32**: 269-306.
- MILLIKEN, G.A., and JOHNSON, D.E. 1984. Analysis of messy data. Vol. I. Designed experiments. Lifetime Learning Publications, Belmont, CA.
- MISPAGEL, M.E., and ROSE, S.D. 1978. Arthropods associated with various age stands of Douglas-fir from foliar, ground and aerial strata. U.S./IBP Coniferous Forest Biome, University of Washington, Seattle.
- NIELSON, B.O. 1978. Above ground food resources and herbivory in a beech forest ecosystem. *Oikos*, **31**: 273-279.
- OHMART, C.P., STEWART, L.G., and THOMAS, J.R. 1983. Leaf consumption by insects in three *Eucalyptus* forest types in southeastern Australia and their role in short-term nutrient cycling. *Oecologia*, **59**: 322-330.
- PRICE, P.W. 1984. *Insect ecology*. 2nd ed. John Wiley and Sons, New York.
- REICHLE, D.E., GOLDSTEIN, R.A., VAN HOOK, R.I., JR., and DODSON, G.J. 1973. Analysis of insect consumption in a forest canopy. *Ecology*, **54**: 1076-1084.
- RISCH, S.J. 1981. Insect herbivore abundance in tropical monocultures and polycultures: an experimental test of two hypotheses. *Ecology*, **62**: 1325-1340.
- SAS INSTITUTE, INC. 1982. SAS user's guide: statistics, 1982 ed. SAS Institute, Inc., Cary, NC.
- SCHOWALTER, T.D. 1986. Ecological strategies of forest insects: the need for a community-level approach to reforestation. *New For.* **1**: 57-66.
- SCHOWALTER, T.D., and CROSSLEY, D.A., JR. 1987. Canopy arthropods and their response to forest disturbance. *In* Forest hydrology and ecology at Coweeta. *Edited by* W.T. Swank and D.A. Crossley. Springer-Verlag, New York. pp. 207-218.
- SCHOWALTER, T.D., WEBB, J.W., and CROSSLEY, D.A., JR. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology*, **62**: 1010-1019.
- SCHOWALTER, T.D., HARGROVE, W.W., and CROSSLEY, D.A., JR. 1986. Herbivory in forested ecosystems. *Annu. Rev. Entomol.* **31**: 177-196.
- SCHOWALTER, T.D., STAFFORD, S.G., and SLAGLE, R.L. 1988. Arboreal arthropod community structure in an early successional coniferous forest ecosystem in western Oregon. *Great Basin Nat.* **48**: 327-333.
- VISSER, J.H. 1986. Host odor perception in phytophagous insects. *Annu. Rev. Entomol.* **31**: 121-144.
- VOEGLIN, D.J. 1982. Invertebrates of the H.J. Andrews Experimental Forest, western Cascade Mountains, Oregon: a survey of arthropods associated with the canopy of old-growth *Pseudotsuga menziesii*. Forest Research Laboratory, Oregon State University, Corvallis.
- WITCOSKY, J.J., SCHOWALTER, T.D., and HANSEN, E.M. 1986. The influence of precommercial thinning on the colonization of Douglas-fir by three species of root-colonizing insects. *Can. J. For. Res.* **16**: 745-749.
- WOLDA, H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. *Ecol. Entomol.* **4**: 181-190.